A taxonomic review of *Satanoperca* (Teleostei: Cichlidae) from French Guiana, South America, with description of a new species

by

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ABSTRACT. - The new species *Satanoperca rhynchitis* occurs in French Guiana in the Oyapock, Approuague, Comté, Kourou, Sinnamary and Iracoubo river drainages. It is distinguished from congeneric species in particular by lower meristics and a longer snout, probably also by red lips in life. Samples of *Satanoperca* from Amapá state in Brazil fall into two groups, one probably representing the Amazonian *S. jurupari*, and the other resembling *S. rhynchitis* but with shorter snout. Species assignation of Amapá samples is not definite because of small sample sizes. Rio Amapá samples and coastal specimens from French Guiana may represent introgression of the Amazonian *S. jurupari*.

RÉSUMÉ. - Une révision taxonomique des *Satanoperca* (Teleostei : Cichlidae) de Guyane française, Amérique du Sud, avec description d'une espèce nouvelle.

La nouvelle espèce *Satanoperca rhynchitis* est distribuée dans les bassins fluviaux de l'Oyapock, de l'Approuague, de la Kourou, du Sinnamary et de l'Iracoubo en Guyane française. Elle se distingue de ses congénères notamment par certains comptes moins élevés et un museau plus long, et probablement aussi, chez les individus vivants, par des lèvres de couleur rouge. Les échantillons de *Satanoperca* de l'état brésilien de l'Amapá se répartissent en deux groupes, l'un représentant vraisemblablement l'espèce amazonienne *S. jurupari*, l'autre ressemblant à *S. rhynchitis* mais avec un museau plus court. Leur assignation spécifique n'est pas encore confirmée à cause de la petite taille des échantillons. Les individus du Rio Amapá et les spécimens côtiers de Guyane française pourraient être introgressés par *S. jurupari*.

Key words. - Oyapock - Approuague - Amapá - *Satanoperca rhynchitis* - *Satanoperca jurupari*.

South American cichlids with a prominent flattened laminar expansion anteroventrally on the first epibranchial are contained in a group currently recognized as a monophyletic tribe Geophagini (Kullander, 1998), alternatively as two lineages within a more expanded Geophagini (López-Fernández *et al*., 2010). This group is quite diverse with eight genera currently recognized, viz. *Apistogramma* Regan, *Apistogrammoides* Meinken, *Biotodoma* Günther, *Geophagus* Heckel, *Gymnogeophagus* Miranda-Ribeiro, *Mikrogeophagus* Meulengracht-Madsen, *Satanoperca* Günther, and *Taeniacara* Myers, with a total of 117 recent species described so far.

Based on information in Keith *et al*. (2000), Kullander (2003), Kullander and Nijssen (1989), Le Bail *et al*. (2012), and Mol *et al*. (2012), 14 species of lobe-bearing geophagins have been reported from the Guianas, almost all of them endemic to Atlantic river drainages. *Apistogramma ortmanni* (Eigenmann) occurs in the Essequibo, Corantijn and Cuyuni rivers, *A. steindachneri* (Regan) in the Mahaica east to the Corantijn drainage, *A. rupununi* Fowler in the Branco and Rupununi rivers, and *A. gossei* Kullander in the Oyapock, Approuague, Comté and Kourou drainages. *Satanoperca leucosticta* (Müller & Troschel) is recorded from the Essequibo, Nickerie and Corantijn rivers, *Geophagus brachybranchus* Kullander & Nijssen from the Nickerie and Corantijn drainages, *G. brokopondo* Kullander & Nijssen from the Suriname River, and *G. surinamensis* (Bloch) from the Coppename, Saramacca, Suriname, Marowijne, and Mana drainages, and coastal rivers in French Guiana. *Geophagus harreri* Gosse is known only from the Marowijne River drainage and *G. camopiensis* Pellegrin only from the Oyapock and Approuague drainages. *Biotodoma cupido* (Heckel) is widely distributed in the Amazon basin and present also in the Essequibo drainage in Guiana.

Puyo (1949) was the first to report the Amazonian species *Satanoperca jurupari (*Heckel) from several localities in the Oyapock River basin in French Guiana. Gosse (1976) reported on a larger number of specimens of *S. jurupari* from the same river and in a statistical comparison of measurements and counts with specimens from the Amazon basin and Guyana + Suriname, he found them significantly different from the other populations and speculated about the possibility to recognize subspecies within *S. jurupari*. Keith *et al*. (2000) reported and illustrated two species of *Satanoperca* from localities in French Guiana east of the Mana River. A relatively slender species was identified as *S.* aff. *jurupari* from the Sinnamary eastward to the Oyapock. A more deep-bodied species was identified as *S. jurupari* from Kaw in French Guiana and from the lower Oyapock at Juminán and Taparabu in Brazil. The slender species

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has been reported in aquarium literature where it is known as "red lips" with reference to a colour character (Weidner, 2000; Stawikowski and Werner, 2004; Aguirre *et al*., 2011). A first examination of material from the Oyapock and Approuague rivers suggested that there is indeed in these drainages a distinct species of *Satanoperca* characterized by relatively small size, low meristics and possibly also colour pattern. Comparison with samples of *Satanoperca* including all known and several undescribed species supported this view. Personal samples from the swamps on the lower Oyapock River also showed clearly the presence of a form agreeing with *S. jurupari* in the Juminán swamps. Additional specimens from the Sinnamary and Kaw, and comparison with a limited number of specimens from the Amapá, Uaçá, and Macari drainages slightly east of the Oyapock, however, suggest a more complex picture. The purpose of this paper is to report on the new species and its delimitation from geographically adjacent samples.

MATERIAL AND METHODS

The procedures for recording measurements and counts are as described by Kullander (1986). Measurements were taken with digital callipers reading to 0.01 mm, rounded to nearest 0.1 mm. Counts were taken under a stereo dissecting microscope, except dorsal and anal fin-ray counts and vertebral counts, which were taken from X-ray radiographs. Vertebral counts include the last half-centrum. Specimen lengths are given as standard length (SL), measured from the tip of the upper jaw to the middle of the base of the caudal fin. Scales in a longitudinal row (E1 row scales) are counted in the row immediately dorsal to that containing the lower lateral line, excluding any that to any extent overlies the pectoral girdle. Scales in a transverse row are counted from that above the first anal-fin spine obliquely dorsorostrad to the dorsal fin. Colour marking terminology follows Kullander (1983, 1986). Measurements and counts are presented in tables I-VIII.

X-radiographs were made on Kodak X-omat V film using a Philips MG-105 low voltage X-ray unit. Morphometric data were managed and analysed using PASW Statistics 18 (SPSS 2009), except that the Principal Component Analysis (PCA) of measurements was made using a separate procedure for component shearing, partialling out multivariate size residues from the second and further components as described by Humphries *et al*. (1981). The PCA was made with log-transformed measurement data to tenth of a millimetre in a covariance matrix, and without rotation. Pelvic-fin length was excluded from the PCA because of the signal of sexual dimorphism in the length of the pelvic fin. Linear regressions were calculated using the Curvefit module in PASW Statistics. Only a subset of the samples examined have georeferenced precise locality information. Spatial point data are given as decimal degrees based on varied sources including maps and original labels.

Specimens studied are deposited in the following institutions: IRSNB, Institut royal des Sciences naturelles de Belgique, Bruxelles; MNHN, Muséum national d'Histoire naturelle, Paris; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; NRM, Swedish Museum of Natural History, Stockholm; NMW Naturhistorisches Museum, Wien; ZMA Zoölogisches Museum, Universiteit van Amsterdam, Amsterdam.

Comparative material

The alpha taxonomy of *Satanoperca* is still largely unresolved and several species await formal description. There is considerable geographical variation in colour within *S. jurupari* auct. as demonstrated by Stawikowski and Werner (2004: 400-417). Unpublished data show extremely little variability in meristics and proportional measurements. Colour pattern, in particular the ornamentation on the head, may be the most important source of species diagnostic characters but is often lost in preservative. Comparative data were sampled here primarily from *Satanoperca jurupari*, including the syntypes and other material from close to the type locality (Manaus). Those samples are generally consistent with data from *Satanoperca* from the rest of the lowland Amazon basin. Comparison was made also with samples from the state of Amapá in Brazil. Data on other species of *Satanoperca* are from Kullander (1986), Kullander and Ferreira (1988), Kullander and Nijssen (1989), and unpublished data.

Satanoperca cf. *rhynchitis*. - All from Brazil, state of Amapá. NRM 12507, 57.6 mm SL, Rio Amapá Grande, cachoeira ca 3 km above the bridge on road BR-156; 2.1399, -51.0207, 21 Aug. 1989, R. Stawikowski & B. Kilian; NRM 19608, 5, 62.1-98.2 mm SL, MZUSP 33137, (7 measured 63.1-91.6 mm SL), MZUSP 40298, 1, 88.9 mm SL, Rio Amapá upstream of Cachoeira Grande, flooded forest; 2.1399, -51.0207, Jan. 1984, M. Goulding.

Satanoperca jurupari from Brazil, state of Amapá. - NRM 12512, 2, 29.7-140.2 mm SL, Rio Uaçá drainage: road BR-156, 75.2 km from Oiapoque, stream and small tributary, tributary to Rio Uruaucá; 2.9866, -51.3756, 19 Aug. 1989, R. Stawikowski; NRM 14845, 1, 71.2 mm SL. Rio Macari drainage: road BR-156, 374.1 km from Oiapoque, small stream flowing to the left; 1.3340, -50.9265, 23 Aug. 1989, R. Stawikowski; NRM 14863, 1, 17.9 mm SL. Rio Oiapoque drainage: road BR-156, 9.1 km from Oiapoque, small stream flowing to the right; 3.8085, -51.7826, 19 Aug. 1989, R. Stawikowski; NRM 28305, 15, 22.1-65.8 mm SL, Rio Oiapoque drainage: savannah igarapé at aldeia Cunene; 4.0189, -51.6183, 28 Mar. 1994, S.O. Kullander & F. Fang.

Satanoperca jurupari from Brazil, state of Amazonas. - IRSNB 17389, 10, 95.8-111.0 mm SL, Parintins, Vila Amazônia; -2.6175, -56.7060, 16 Dec. 1967, Léopold III & J.P. Gosse; NMW 23580, 1, 152.2 mm SL, Mouth of Rio Negro; about -3.1567, -59.9772, No date, J. Natterer. Syntype of *Geophagus jurupari*; NRM 17003, 1, 159.6 mm SL, Lago Janauacá; -3.5000, -60.6667, 17 Sep. 1980, S.O. Kullander *et al*.; NRM 17004, 2, 134.3-155.5 mm SL, Whitewater River in vicinity of Manaus; about -3.1939, -60.0656, 27 Nov. 1923, D. Melin *et al*.; NRM 17010, 1, 60.0 mm SL, Lago Janauari; -3.2154, -60.0248, 9 Sep. 1980, S.O. Kullander *et al*.

***Satanoperca rhynchitis*, new species**

(Tabs I, IV-X; Figs 1-4)

Material examined

Holotype. - IRSNB 881. An adult male, 104.9 mm SL. French Guiana, Crique Sikini, left bank tributary to Oyapock

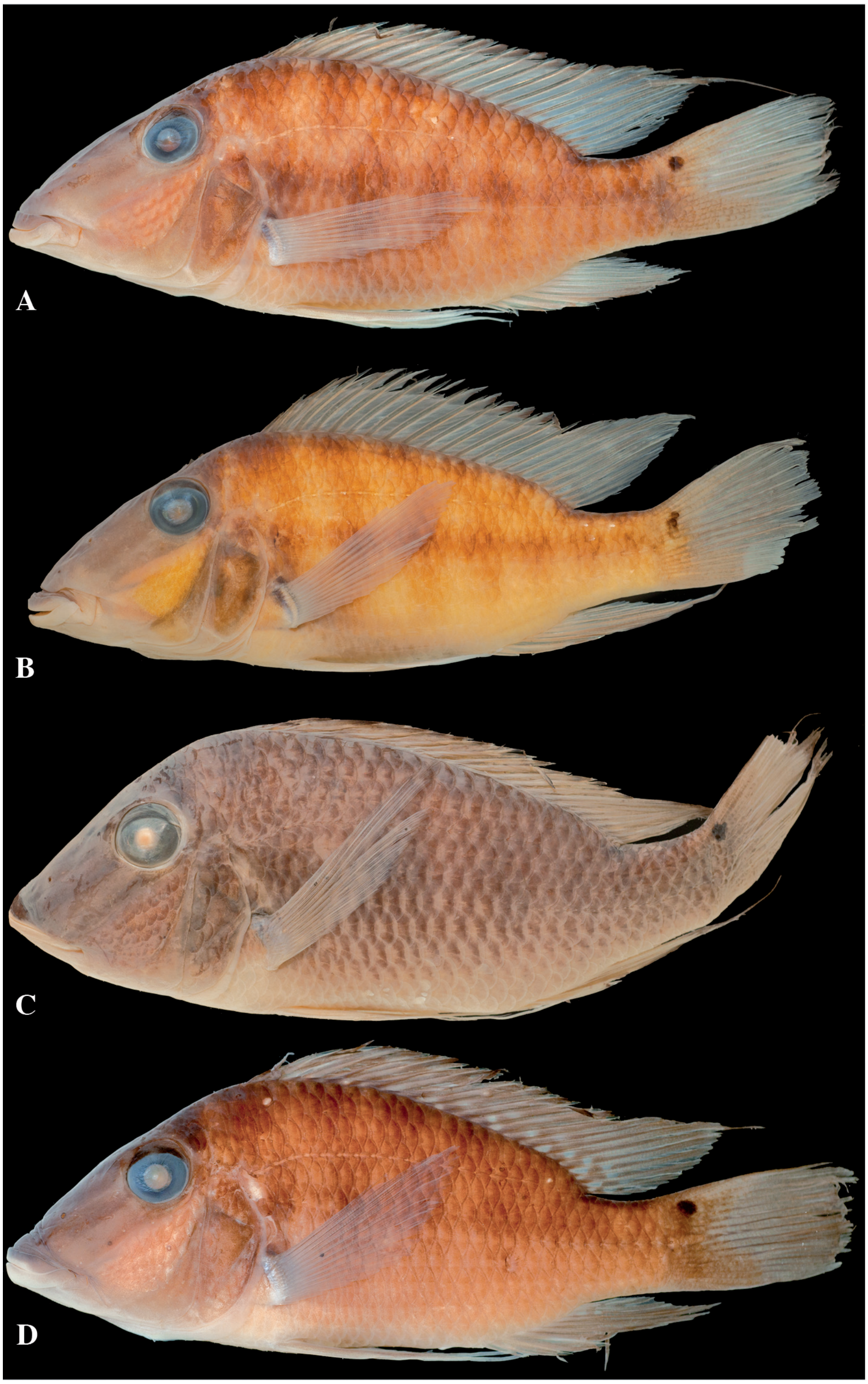

Figure 1. - **A**: *Satanoperca rhynchitis*. Holotype, IRSNB 888, adult male, 104.9 mm SL. French Guiana, Crique Sikini, left bank tributary to Oyapock River. **B**: *Satanoperca rhynchitis*. NRM 48368. 98.4 mm SL. Approuague River. **C**: *Satanoperca jurupari*. NRM 12512, 140.2 mm SL. Brazil, State of Amapá, Uaçá River. **D**: *Satanoperca* cf. *rhynchitis*. MZUSP 40298, 88.9 mm SL. Brazil, State of Amapá, Rio Amapá.

River; 3.2513, -52.2573. 6 Dec. 1969. Léopold III & J.P. Gosse.

Paratypes. - All from French Guiana: Oyapock River drainage: IRSNB 882-888, 7, 84.6-128.1 mm SL, Same data as holotype; NRM 48367, 2, 97.4-99.8 mm SL, Same data as holotype; ZMA 107.643, 1, 101.0 mm SL, Crique Gabaret near its mouth into Oyapock River; 3.9072, -51.7943, 11-14 Nov. 1976, F. d'Aubenton; ZMA 107.703, 1, 141.0 mm SL, Saut Ako; 2.77, -52.48, 25 Sep. 1976, F. d'Aubenton; Approuague River drainage: NRM 29452, 3, 70.0-84.9 mm SL, Approuague, 26 Jun. 1986. P. Planquette; NRM 29484, 1, 91.8 mm SL, Approuague River, Mar. 1983, P.Y. Le Bail; NRM 48368, 1, 98.4 mm SL, Approuague, Apr. 1983, P.Y. Le Bail; Kaw swamps: NRM 41112, 3, 91.9-119.9 mm SL, Kaw; 4.4833, -52.0333, Jun. 1985, Collector not stated; Comté River drainage: NRM 18185, 8, 25.7-116.0 mm SL, Rivière Grand Bagot, downstream Bagot, at sand banks; 4.5333, -52.5333, 31 Aug.-1 Sep. 1992, J. Westin; NRM 29467, 2, 69.5-95.9 mm SL, Sinnamary River, Petit Saut; 5.0817, -53.0500, May 1984, P. Planquette; Kourou River drainage: NRM 27805, 27 (1 measured, 81.0 mm SL), Crique Soumouro where crossing N.1, 20 Mar. 1994, 5.1250, -52.7308, S.O. Kullander & F. Fang; Iracoubo River drainage: MNHN uncat., 1, 95.2 mm SL, NRM 29500, 115.4 mm SL, Iracoubo; 5.4767, -53.2133, 28 Apr. 1986, P. Planquette; Sinnamary River drainage: MNHN uncat., 1, 114.1 mm SL, NRM 29441, 1, 117.9 mm SL, Sinnamary River, Saut Caouenne [=Saut Kawènn]; 4.8769, -53.0561, 4 Aug. 1982, P. Planquette.

Non-types. - Locality information missing. NRM 29496, 1, 116.4 mm SL, French Guiana [Oyapock or Approuague], No date, P. Planquette.

Diagnosis

Satanoperca rhynchitis differs from *S. daemon* (Heckel), *S. lilith* Kullander & Ferreira, and *S. acuticeps* (Heckel) in the absence of well defined dark blotches on the side, and lower meristics (soft dorsal-fin rays 8-10, modally 9, *vs* 12-14; E1 scales 25-27, modally 26, *vs* 27-31; ceratobranchial gill-rakers 12-14, modally 14, *vs* 17-23). It is similar to remaining species of the genus, *S. jurupari*, *S. leucosticta* (Müller & Troschel), *S. mapiritensis* (Fernández-Yépez), and *S. pappaterra* (Heckel) in meristics, proportional measurements, dentition, and general colour pattern, but can be distinguished from all by fewer scales in the E1 row, 25-26, rarely 27, *vs* 27-28. It differs also from *S. pappaterra* in the Guaporé and Paraguay River basins in the absence of prominent black blotches along the base of the dorsal fin, and absence of a well-defined black band along the middle of the side. It can be distinguished from *S. leucosticta* (Guyana and Suriname), and *S. mapiritensis* (Orinoco river drainage) by the absence of white spots on the snout and sides of the head. The most similar species may be *S. jurupari* in the central Amazon basin from which it differs in modal dorsal-fin count XV.9, *vs* XV.10, E1 scale count 26 *vs* 27, gill-raker count 13-14 (rarely 15) *vs* 16-17 (rarely 14, 15, 18), gill blade narrower than ceratobranchial (*vs* wider), and generally longer snout (14.3-19.4% of SL, *vs* 11.3-15.9%).

Description

Based on the holotype with notes on variation; measurements from 27 specimens are summarized in table I; meristics is summarized in tables IV-IX. See Figure 1A, B for general aspect.

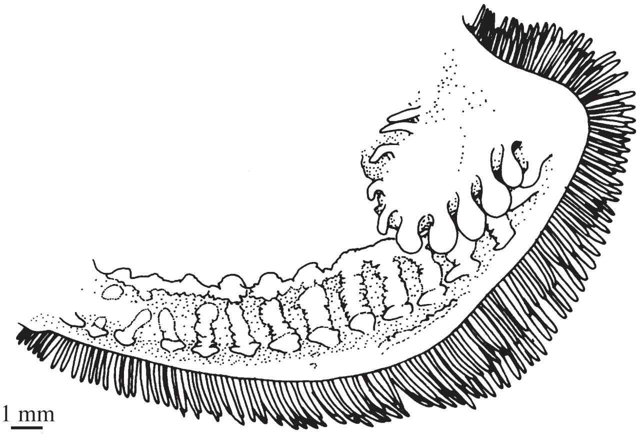

Figure 2. - *Satanoperca rhynchitis*, NRM 48367, 97.4 mm SL. First gill arch in lateral aspect.

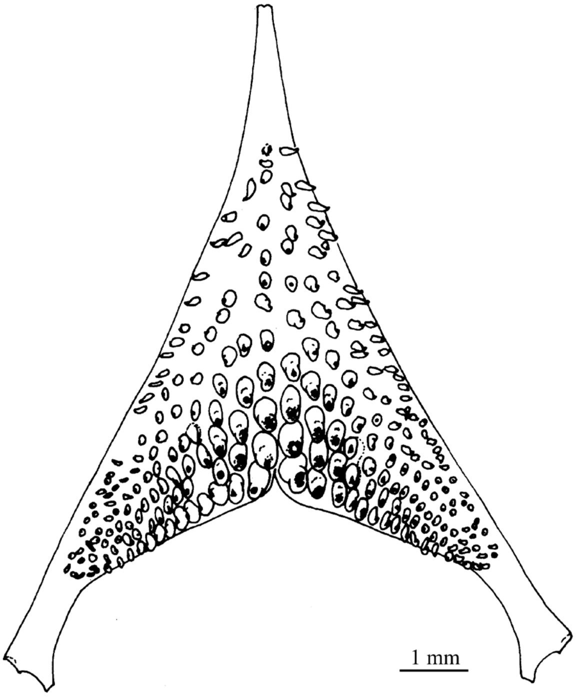

Figure 3. - *Satanoperca rhynchitis*, NRM 48367, 97.4 mm SL. Lower pharyngeal jaw in occlusal aspect.

Table I. - Standard length (in mm) and proportional measurements in percents of standard length of *Satanoperca rhynchitis*. SD = standard deviation. Regression line parameters, a (intercept), b (slope), and r (Pearson's correlation coefficient) are calculated from measurements expressed in millimetres. Data from the holotype are given separately and also included in calculated sample values.

	n	Holotype	Min	Max	Mean	SD	a	b	r
Standard length (mm)	27	104.9	69.5	141.0	101.6	17.44			
Head length	27	36.9	32.9	39.5	36.3	1.62	0.109	0.362	0.965
Snout length	27	18.0	14.3	19.4	16.9	1.38	-2.221	0.191	0.928
Body depth	27	39.4	37.4	42.8	39.1	1.28	-0.889	0.400	0.984
Orbit diameter	27	10.4	9.4	11.9	10.9	0.58	-1.668	0.092	0.951
Head width	27	16.0	15.3	16.9	16.1	0.46	-0.248	0.164	0.988
Interorbital width	27	9.2	8.1	10.3	8.9	0.66	-0.248	0.164	0.96
Preorbital depth	27	14.3	11.5	16.2	14.4	1.08	-2.111	0.111	0.98
Caudal peduncle depth	27	13.4	12.9	15.0	13.9	0.47	-1.151	0.150	0.991
Caudal peduncle length	27	14.3	13.4	16.0	14.8	0.77	0.483	0.143	0.958
Pectoral-fin length	27	33.8	31.5	36.7	33.6	1.36	-3.054	0.367	0.977
Pelvic-fin length	27	34.3	28.6	48.7	35.4	4.54	-10.869	0.464	0.88
Last dorsal-fin spine length	26	18.1	16.9	19.6	18.2	0.74	0.151	0.180	0.971

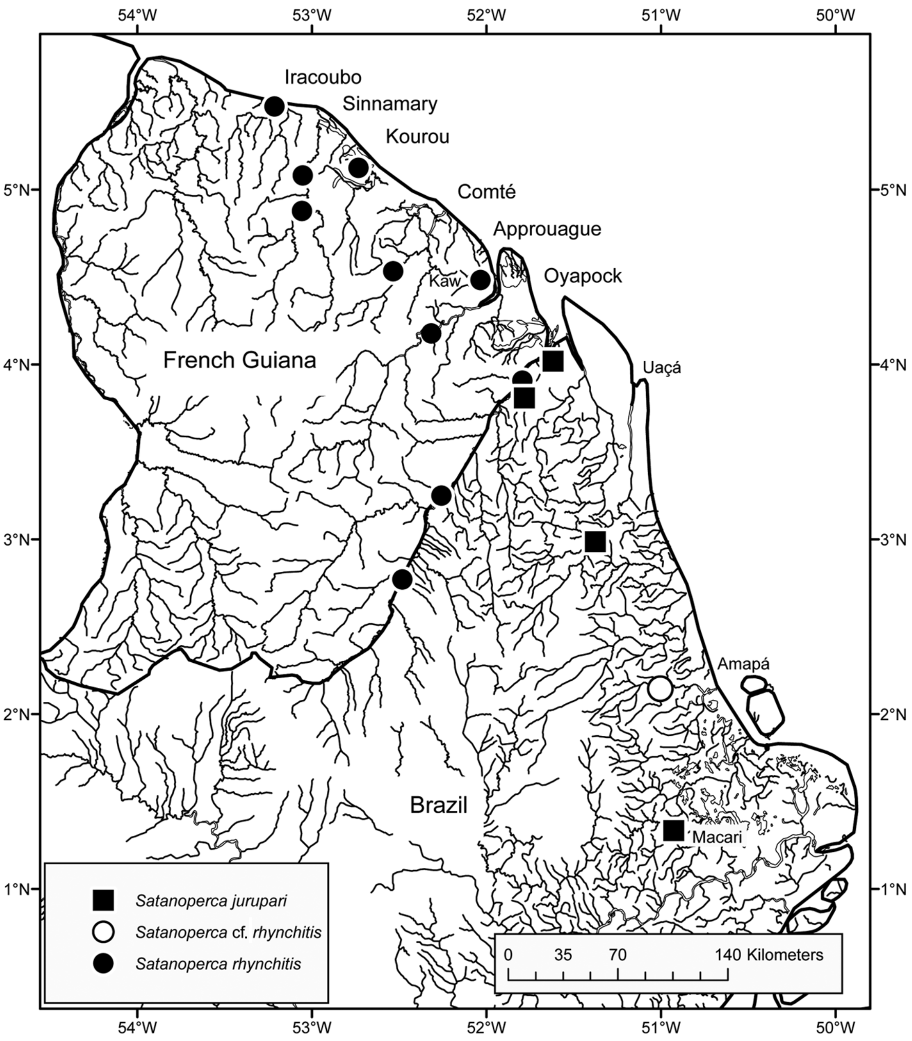

Figure 4. - Map of French Guiana and adjacent Brazil, showing collecting localities of *Satanoperca*.

Elongate, laterally compressed. Dorsal contour more arched than ventral. Frontal contour ascending straight or with slight indentation above eye. Snout long, pointed in lateral aspect. Mouth below level of lower lateral line, wider than interorbital space. Tip of maxilla reaching slightly beyond vertical from nostril. Lips thick, with wide folds; upper continued by wide median fold across symphysis; lower with groove symphysially separating lip from lower jaw. Supracleithrum serrated in two specimens. Cleithrum with irregular margin but smooth in all specimens.

Scales in transverse row 7+1+2 1/2, occasionally 2 above lateral line; circumpeduncular scale rows 16. Scales ctenoid on sides and predorsally, cycloid on lower about half of cheek, on sub- and interopercle and preventrally except close to pelvic-fin bases. Cheek scale rows 4-5. Lateral line scales 17-19/8-10, plus two tubed scales continuing lower lateral line on caudal fin. Scales between upper lateral line and dorsal fin 3 1/2 anteriorly, 1 1/2 posteriorly. Caudal-fin squamation extending to about middle of fin marginally.

First dorsal-fin spine about 1/3 length of last; spines subequal in length from 5th or slightly shorter from 8th to penultimate, last longest; soft part pointed, usually with prolonged 4th ray which may reach to slightly beyond caudal fin. Soft anal fin pointed, reaching to 1/3 of caudal fin or slightly beyond. Pectoral fin with rounded tip, reaching to above second spine to first ray of anal fin, rarely slightly shorter. Pelvic fin pointed, with first ray produced reaching at most to beginning of caudal peduncle. Caudal fin truncate or subtruncate.

Gill rakers externally on first gill arch 9-12 epibranchial, 1 in angle and 12-15 ceratobranchial. Gill filaments short, gill blade narrower than gill arch (Fig. 2) except in one specimen (NRM 41112, 119.9 mm SL) in which gill blade wider than gill arch. Microbranchiospines present externally on 2nd to 4th arches, internally on 2nd and 3rd arches, internally on 4th arch in five specimens only; one Approuague specimen with microbranchiospines only externally on 3rd and 4th arches.

Lower pharyngeal tooth plate (Fig. 3) moderately elongate; anterior teeth slender, unicuspid, cusp anteriad curved, otherwise with posterior antrorse cusp and small projection subapically on rostral margin, medioposterior teeth much stronger than the rest, with blunt or worn low posterior cusp and very narrow anterior shelf. Vertebrae 14 + 13 = 27 (3), 14 + 14 = 28 (15).

Teeth in outer or only hemiseries of upper/lower jaw 18-29/10-20; a single row in upper jaw; an inner row anteriorly in lower jaw rarely absent; one Approuague specimen exceptional in having a few inner teeth in upper jaw and two inner rows anteriorly in lower jaw.

Table II. - Standard length (in mm) and proportional measurements in percents of standard length of *Satanoperca* from Amapá localities. SD = standard deviation. Regression line parameters, a (intercept), b (slope), and r (Pearson's correlation coefficient) are calculated from measurements expressed in millimetres.

	n	min	max	mean	SD	a	b	r
Standard length (mm)	17	62.1	140.2	82.6	18.84			
Head length	17	33.0	36.4	35.1	0.86	2.528	0.319	0.994
Snout length	17	13.1	15.9	14.6	0.82	-0.053	0.147	0.971
Body depth	17	37.5	42.4	40.0	1.13	0.747	0.390	0.993
Orbit diameter	17	10.4	12.5	11.4	0.59	1.642	0.093	0.989
Head width	17	14.7	16.8	15.8	0.62	0.216	0.155	0.986
Interorbital width	17	8.1	10.4	8.8	0.62	-2.194	0.115	0.978
Preorbital depth	17	12.0	15.3	13.2	0.80	-3.275	0.173	0.994
Caudal peduncle depth	17	13.6	15.7	14.2	0.52	-0.082	0.143	0.989
Caudal peduncle length	17	12.2	15.9	14.1	0.94	-2.842	0.176	0.989
Pectoral-fin length	17	33.3	36.6	34.6	0.93	-0.885	0.357	0.995
Pelvic-fin length	17	31.1	43.6	35.2	3.25	-12.549	0.510	0.985
Last dorsal-fin spine length	15	16.6	20.7	18.9	1.08	2.119	0.162	0.955

Table III. - Standard length (in mm) and proportional measurements in percents of standard length of *Satanoperca jurupari* from the Central Amazon basin near Manaus. SD = standard deviation. Regression line parameters, a (intercept), b (slope), and r (Pearson's correlation coefficient) are calculated from measurements expressed in millimetres. The syntypes are included in calculated values.

	n	min	max	Mean	SD	a	b	r
Standard length (mm)	15	60.0	159.6	113.7	26.48			
Head length	15	31.6	34.7	33.1	0.88	2.528	0.319	0.995
Snout length	15	11.3	15.9	14.3	0.97	-0.53	0.147	0.986
Body depth	15	39.1	43.5	41.1	1.33	0.747	0.390	0.989
Orbit diameter	15	8.8	12.2	9.9	0.69	1.642	0.930	0.977
Head width	15	14.8	17.2	15.8	0.65	0.216	0.155	0.989
Interorbital width	15	9.3	11.4	10.4	0.49	-2.194	0.115	0.983
Preorbital depth	15	11.2	15.7	13.9	1.08	-3.275	0.173	0.988
Caudal peduncle depth	15	13.2	15.9	14.7	0.68	-0.820	0.143	0.975
Caudal peduncle length	15	12.0	15.7	13.3	1.09	-2.842	0.176	0.961
Pectoral-fin length	14	34.0	37.5	35.4	1.14	-0.885	0.357	0.992
Pelvic-fin length	14	35.3	47.6	42.5	3.91	-12.549	0.510	0.891
Last dorsal-fin spine length	15	17.1	22.0	18.7	1.34	2.119	0.162	0.967

Colouration

Chest, abdomen, underside of head greyish white; intermandibular area and ventral part of branchiostegal membrane greyish. Sides pale brownish yellow. Cheek scales in some specimens light with contrasting brown margin, in others cheek uniformly brownish. Gill cover brownish yellow. Snout and lachrymal dark grey. Two distinct black interorbital stripes; two lachrymal stripes indicated in some specimens. No light or silvery spots on head. Dark brown stripe bordering orbit posterodorsally. Brownish markings on sides include an indistinct lateral band on E1 and 1/3 to 1/2 of row 0 scales, and 7 vertical bars reaching ventrally to pectoral axilla level. Scales of dorsal side with a narrow brown margin. Dorsal margin and inner face of pectoral-fin base blackish. Dorsal fin smoky, lappets dark grey or blackish; light spots on soft part absent or faint. Anal fin smoky, lower margin darker, immaculate. Pelvic fin smoky, outer margin

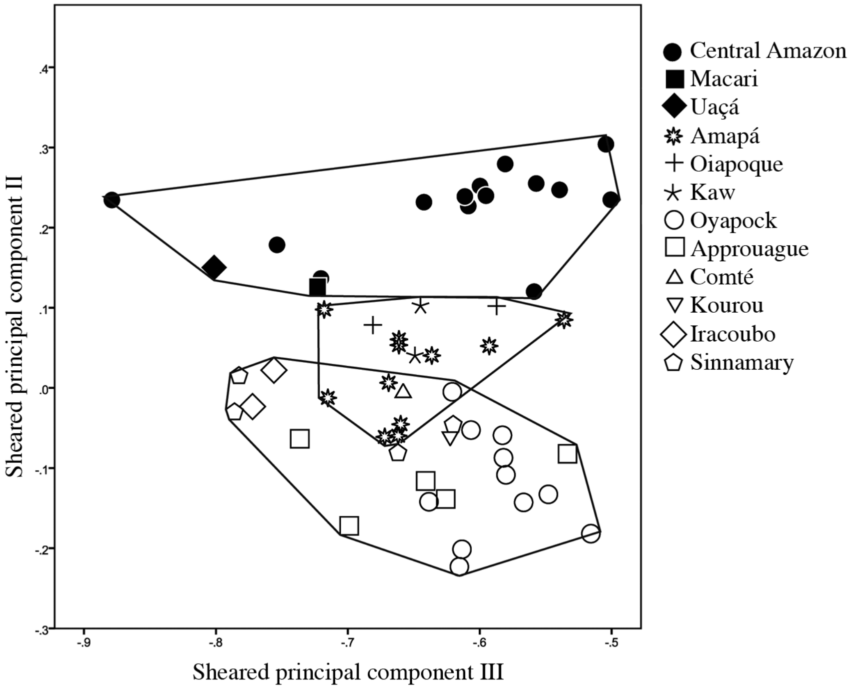

Figure 5. - Plot of scores of second and third sheared principal components of pooled measurement data from *Satanoperca* from French Guiana and the state of Amapá, labelled with river name, and Central Amazonian *S. jurupari*. Enclosures identify *S. jurupari* (top), potential intermediate samples, and *S. rhynchitis*.

Table IV. - Absolute frequency of E1 scale counts in *Satanoperca rhynchitis*, *S. jurupari*, and *Satanoperca* from Amapá. Modal values in bold. Asterisk marks *S. rhynchitis* holotype value.

	25	26	27	28
S. jurupari Central Amazon		1	**11**	3
S. jurupari Macari		**1**		
S. jurupari Uaçá		**1**	**1**	
S. jurupari Oiapoque		3	**9**	
S. cf. *rhynchitis* Rio Amapá		5	**7**	1
S. rhynchitis Oyapock	2	**9***		
S. rhynchitis Approuague		**5**		
S. rhynchitis Kaw		**3**		
S. rhynchitis Comté		**6**	1	
S. rhynchitis Kourou		**1**		
S. rhynchitis Iracoubo		**2**		
S. rhynchitis Sinnamary		**3**	1	

Table V. - Absolute frequency of cheek scale row counts in *Satanoperca rhynchitis*, *S. jurupari*, and *Satanoperca* from Amapá. Modal values in bold. Asterisk marks *S. rhynchitis* holotype value.

	4	5	6	8
S. jurupari Central Amazon		2	**12**	1
S. jurupari Macari			**1**	
S. jurupari Uaçá		**1**		
S. jurupari Oiapoque		**2**		
S. cf. *rhynchitis* Rio Amapá	1	**11**	1	
S. rhynchitis Oyapock	**6***	**6**		
S. rhynchitis Approuague	**2**	**2**	1	
S. rhynchitis Kaw		**3**		
S. rhynchitis Comté	**1**			
S. rhynchitis Kourou		**1**		
S. rhynchitis Iracoubo	**2**			
S. rhynchitis Sinnamary	**4**			

of first ray white. Caudal fin brownish yellow basally, naked portion smoky, a few short streaks of darker pigment usually present on interradial membranes, occasionally indistinct light dots. Caudal spot dark brown, roundish, crossing rays D4-D6, with or without lighter surrounding area.

Living specimens (Weidner, 2000: 341; Stawikowski and Werner, 2004: 410; Aguirre *et al.*, 2011: 170-185) similar in colour pattern to preserved specimens, but with reddish lips and fins except pectoral fin with blue and red thin stripes. The body colour is predominantly pale greyish to yellowish with silvery reflections on body scales.

Geographical distribution and habitats

Known only from the Oyapock, Approuague (including Kaw), Kourou, Comté, Iracoubo, and Sinnamary drainages in French Guiana (Fig. 4).

Etymology

Rhynchitis refers to the long snout of the species and is a substantivated adjective, to be considered as a noun in apposition, formed from the noun rynchos/rhynchos (Greek), snout, and the adjectival suffix -itis (Greek), expressing possession.

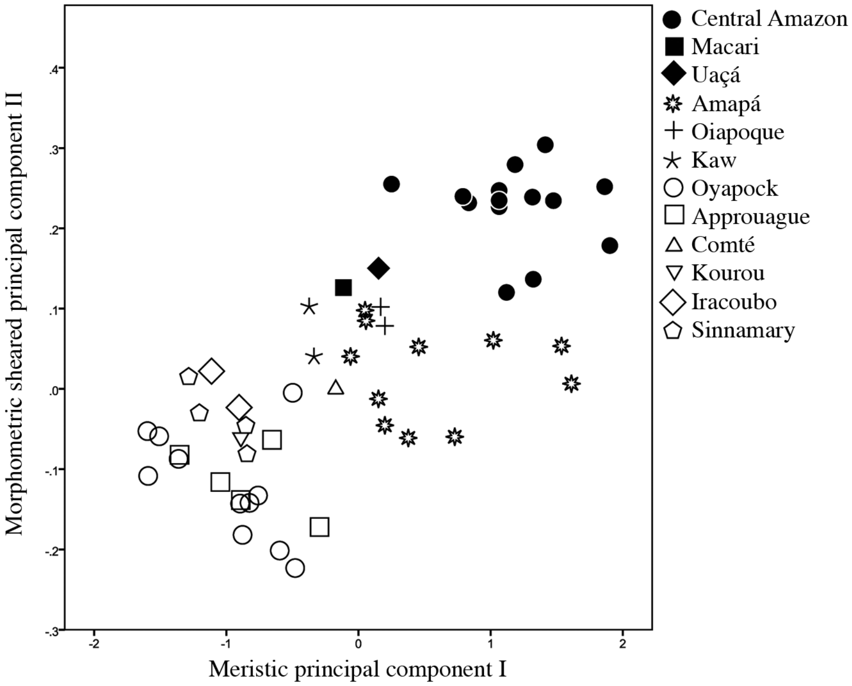

Figure 6. - Plot of scores of second sheared principal components of pooled measurement data on first principal component of pooled meristic data from *Satanoperca* from French Guiana and the state of Amapá, labelled with river name, and Central Amazonian *S. jurupari*.

Comparative morphology

Specimens from the Oyapock and Approuague drainages were recognized as distinct from all other species of *Satanoperca* in which white spots are absent from head sides by the proportionally long snout, supported by low meristics (E1 scales, dorsal-fin rays, and gill rakers), shared with other samples from French Guiana in which the relative snout length is variable. All specimens with low meristics from the Oyapock, Approuague, Comté, Sinnamary, and Iracoubo rivers, and Kaw, were thus assigned to a single sample (*S. rhynchitis*), based on location and low meristics. Scattered samples available from Amapá (Fig. 1C-D, Tab. II) and specimens from the Central Amazon (Tab. III) were included as putative representatives of *S. jurupari*. Samples were labelled by locality, and recognition of phenotypes follows the weighed information from meristics and principal component analysis.

The morphological Principal Component Analysis (Fig. 5) shows a stratification topped by Central Amazonian specimens with some outliers that marginally include Macari and Uaçá specimens. Oyapock and Approuague specimens mainly cluster together, and there is quite some overlap with specimens from the Rio Amapá, which otherwise, like Kaw and Juminán specimens are positioned in between the French Guiana and Central Amazonian specimens. The combined morphometric and meristic PCA orders samples along both axes showing a correlation between meristic and morphometric data (Fig. 6). Meristic components are dominated by gill rakers, E1 scales, dorsal fin counts, and pectoral fin counts, and the first component reflects diagnostic numbers of gill rakers, E1 scales and soft dorsal fin rays in *S. rhynchitis* (Tab. XI).

Most morphometric variation in the pooled sample is in snout length, interorbital width and caudal peduncle length

Table VI. - Absolute frequency of lateral line scales counts in *Satanoperca rhynchitis*, *S. jurupari* and *Satanoperca* from Amapá. Modal values in bold.

Upper	15	17	17	17	17	18	18	18	19	19	19	19	19	20	20	20	20
Lower	11	9	10	11	13	9	10	11	8	9	10	11	12	8	10	11	12
Central Amazon							1				3	**4**	3		2	1	1
Macari								1									
Uaçá					1												
Amapá						1	2			1	**6**				1	2	
Oiapoque											1			1			
Oyapock		**2**	1			**2**	**2**		**2**	1	1						
Approuague				**1**		**1**	**1**	**1**			**1**						
Kaw								2				1					
Comté				1													
Kourou				1													
Iracoubo				1				1									
Sinnamary	1					1	2										

Table VII. Absolute frequency of dorsal fin-ray counts in *Satanoperca rhynchitis*, *S. jurupari* and *Satanoperca* from Amapá. Modal values in bold.

Spines	14	14	15	15	15	15	16	16	16
Rays	9	11	8	9	10	11	8	9	10
Central Amazon		1			**9**	2		1	2
Macari				**1**					
Uaçá				**1**	**1**				
Amapá		1		2	**8**				2
Oiapoque				1	4		1	**9**	1
Oyapock			2	**10**					
App	1			**4**					
Kaw				**3**					
Comté				**4**	3			1	
Kourou				**1**					
Iracoubo				**2**					
Sinnamary				**3**	1				

(Tab. X). Specimens from Uaçá and the Central Amazon tend to have shorter snouts and wider interorbital space than those from French Guiana (Figs 7-9). French Guiana specimens over 100 mm SL are separated from Central Amazon, Uaçá, and large Sinnamary specimens by longer snout (Fig. 8), whereas smaller specimens are similar in snout length, and a similar pattern is seen in interorbital width, but with greater interorbital space in Central Amazon specimens (Fig. 7). The caudal peduncle/standard length ratio tends to be higher (shorter caudal peduncle) in Amazonian specimens, but variation is considerable in this measurement.

DISCUSSION

Satanoperca was first diagnosed by Günther (1862: 312) as having the eye behind the middle of the length of the head and fins without scales on the dorsal fin in distinction from *Geophagus* with shorter snout and scaly fins. The genera were merged under *Geophagus* by Regan (1906), and Gosse (1976). *Satanoperca* was revalidated by Kullander (1986) with a number of diagnostic characters expanded on by Kullander and Nijssen (1989) and Kullander (1998). Externally, species of *Satanoperca* are readily distinguished by the presence of an ocellated blotch dorsally at the base of the caudal fin, a colour marking common among South American cichlids, but absent in all other Geophaginae *sensu* Kullander (1998).

Seven species of *Satanoperca* have been described so far: *S. daemon*, type species of the genus, *S. acuticeps*, *S. jurupari*, *S. leucosticta*, *S. lilith*, *S. mapiritensis*, and *S. pappaterra*. *Satanoperca macrolepis* Günther, was synonymised with *S. leucosticta* by Kullander and Nijssen (1989).

Species of *Satanoperca* occur in most cis-Andean river systems, including all of the Orinoco, Amazon, and Tocantins basins, the upper Paraguay basin, and, probably introduced,

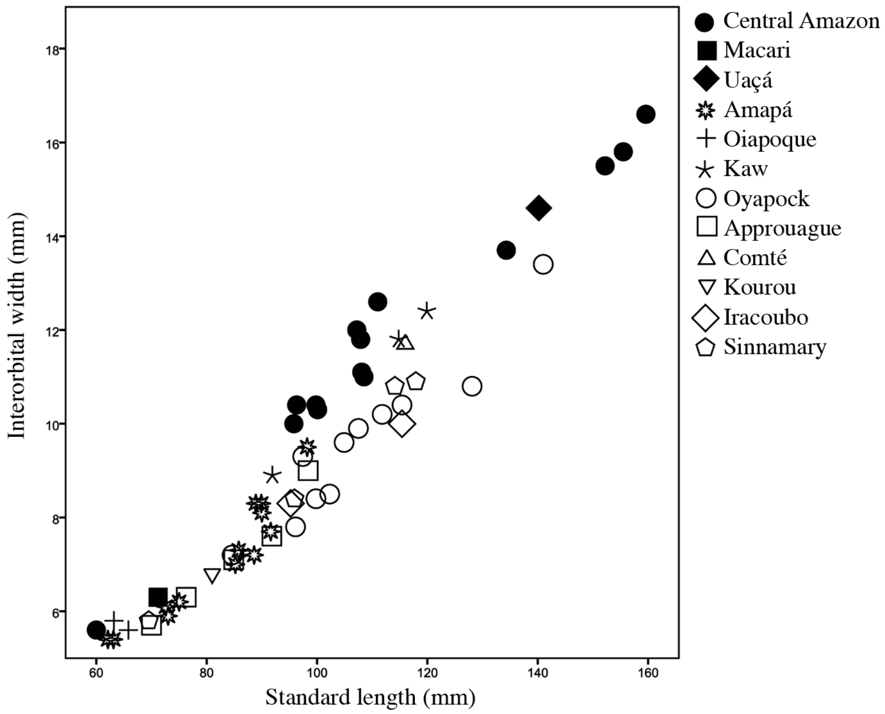

Figure 7. - Interorbital width plotted against standard length. Data from *Satanoperca* from French Guiana and the state of Amapá, labelled with river name, and Central Amazonian *S. jurupari*.

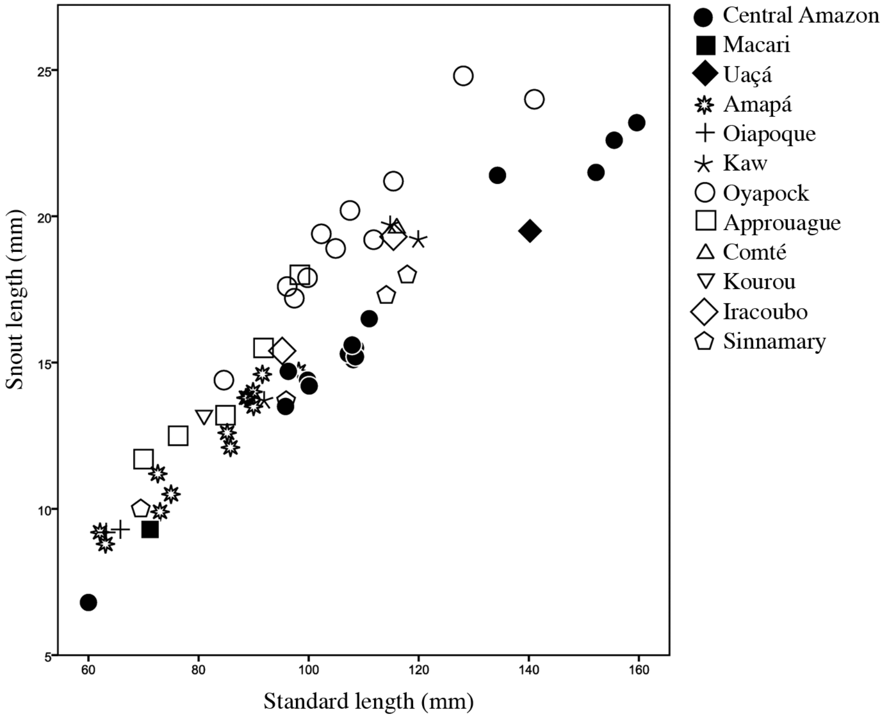

Figure 8. - Snout length plotted against standard length. Data from *Satanoperca* from French Guiana and the state of Amapá, labelled with river name, and Central Amazonian *S. jurupari*.

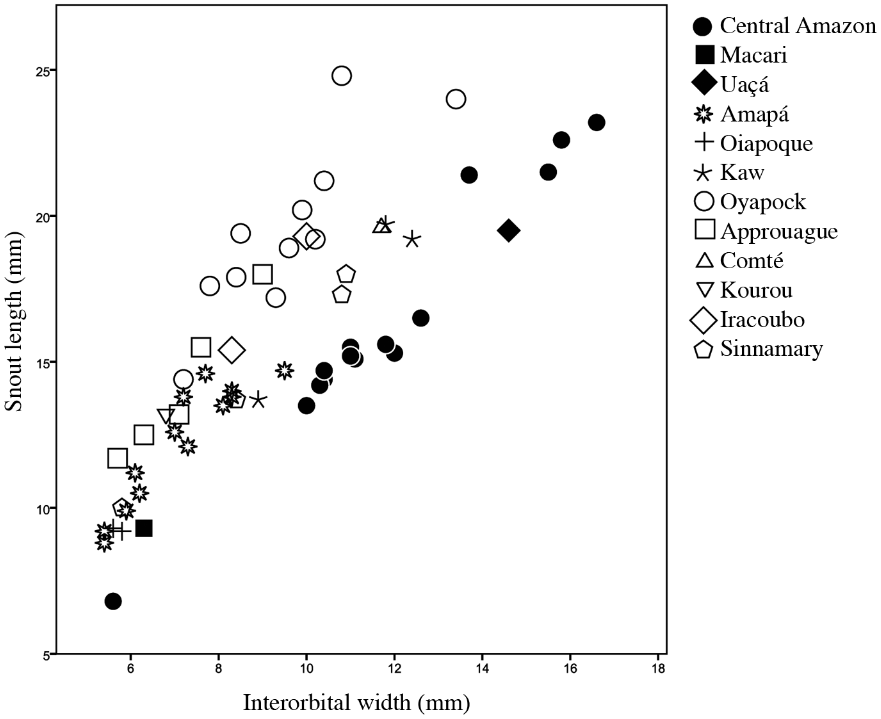

Figure 9. - Snout length plotted against interorbital width. Data from *Satanoperca* from French Guiana and the state of Amapá, labelled with river name, and Central Amazonian *S. jurupari*.

in the Rio Paraná in Brazil and adjacent Paraguay. The genus is absent from coastal Atlantic rivers south of the mouth of the Amazon, but present in the state of Amapá. It is recorded from coastal rivers of Suriname and Guyana. There is even a record from the Rio Tumbes on the Pacific slope of Peru (Chirichigno, 1963), which, however, seems to be in error. In French Guiana, there are records from the Oyapock River west to the Sinnamary River, but the genus is apparently completely absent from the Maroni River drainage (Kullander and Nijssen, 1989; Keith *et al.*, 2000; Le Bail *et al.*,

Table VIII. - Absolute frequency of pectoral and anal fin-ray counts in *Satanoperca rhynchitis*, *S. jurupari*, and *Satanoperca* from Amapá. Modal values in bold. Asterisk marks *S. rhynchitis* holotype value.

	Pectoral-fin rays		Soft anal-fin rays		
	13	14	6	7	8
S. jurupari Central Amazon		**15**	1	**14**	
S. jurupari Macari	1			**1**	
S. jurupari Uaçá	**1**	**1**		**2**	
S. jurupari Oiapoque		**2**		**2**	
S. cf. *rhynchitis* Rio Amapá	2	**11**		**11**	2
S. rhynchitis Oyapock	4	**8***	1	**11***	
S. rhynchitis Approuague	2	**3**	2	**3**	
S. rhynchitis Kaw	1	**2**	1	**2**	
S. rhynchitis Comté		**1**		**1**	
S. rhynchitis Kourou	**1**		1		
S. rhynchitis Iracoubo		**2**		**3**	
S. rhynchitis Sinnamary	**4**			**2**	

Table IX. - Absolute frequency of ceratobranchial gill-raker counts in *Satanoperca rhynchitis*, *S. jurupari*, and *Satanoperca* from Amapá. Modal values in bold. Asterisk marks *S. rhynchitis* holotype value.

	12	13	14	15	16	17	18
S. jurupari Central Amazon			1	2	**8**	3	1
S. jurupari Macari					**1**		
S. jurupari Uaçá				**1**			
S. jurupari Oiapoque			1	1			
S. cf. *rhynchitis* Rio Amapá				5	**7**	1	
S. rhynchitis Oyapock	1*	4	**7**				
S. rhynchitis Approuague		**2**	**2**	1			
S. rhynchitis Kaw			**2**	1			
S. rhynchitis Comté			**1**				
S. rhynchitis Kourou			**1**				
S. rhynchitis Iracoubo		**1**	**1**				
S. rhynchitis Sinnamary		**2**	1	1			

Table X. - Variable loadings on principal components 1–3 and sheared components 2–3 from pooled morphological dataset of *Satanoperca rhynchitis*, *S. jurupari*, and *Satanoperca* from Amapá. Highest loadings in bold.

	I	II	Sheared II	III	Sheared III
SL	0.277	0.049	0.052	-0.062	-0.059
Head length	0.269	-0.260	-0.256	0.094	0.096
Snout length	0.324	**-0.563**	**-0.559**	0.466	0.470
Body depth	0.279	0.242	0.245	0.028	0.031
Orbital diameter	0.218	-0.209	-0.206	-0.195	-0.193
Head width	0.271	0.043	0.046	0.031	0.034
Interorbital width	0.340	**0.561**	**0.565**	0.060	0.063
Preorbital depth	0.355	-0.148	-0.143	0.185	0.188
Caudal-peduncle depth	0.281	0.280	0.283	0.078	0.081
Caudal-peduncle length	0.279	-0.254	-0.251	**-0.815**	**-0.812**
Pectoral-fin length	0.282	0.165	0.169	0.074	0.077
Last dorsal-fin spine length	0.262	0.050	0.053	-0.130	-0.128
Eigenvalue	0.694	0.020	N/A	0.007	N/A
Cumulative Variance %	95.00	97.80	N/A	98.60	N/A

Table XI. - Variable loadings on principal components 1-3 from pooled meristic dataset of *Satanoperca rhynchitis*, *S. jurupari*, and *Satanoperca* from Amapá. Highest loadings in bold.

	I	II	III
Gill rakers	**0.826**	-0.107	-0.126
Lower lateral line scales	0.492	-0.539	0.337
Upper lateral line scales	0.674	0.362	-0.341
E1 scales	**0.805**	0	0.364
Pectoral-fin rays	0.469	-0.041	**-0.669**
Dorsal-fin soft rays	0.758	-0.383	0.050
Dorsal-fin spines	0.264	**0.806**	0.319
Cheek scale rows	0.725	0.285	0.092
Eigenvalue	3.415	1.311	0.939
Cumulative variance %	42.69	59.08	70.81

2012; Mol *et al.*, 2012).

Satanoperca includes three morphologically distinctive groups of species, which may be referred to as the *S. jurupari* group, the *S. daemon* group, and the monotypic *S. acuticeps* group. Species of the *S. daemon* and *S. jurupari* groups are similar in body shape, and in the relatively long snout with the mouth very low, and the lower jaw slightly projecting. Species of the *S. daemon* group grow very large, and are characterized by one or two large dark blotches on the side and a prominent ocellus at the base of the caudal fin. They have 29-31 scales in the E1 row, and dorsal fin count usually XIV.13 (XII-XIV.12-14). Gill raker numbers range from 18 to 22. *Satanoperca acuticeps* has a forwardly directed mouth, usually XIII.12 (XIII.11-12) dorsal-fin rays, 27-28 E1 scales and 17-20 gill rakers.

Species of the *S. jurupari* group show a dark horizontal band or row of blotches along the middle of the side. The dorsal fin count is usually XV.10 (XIV-XVII.8-11) and the scale count usually 27 (26-28). Gill-raker numbers range between 12 and 18. There are four valid species described in the *S. jurupari* group. *Satanoperca jurupari* was described from near Manaus, and this name is applied on samples from the lower Rio Negro, Amazonas and Solimões. Kullander (1986) described *S. jurupari* from the Peruvian and Bolivian Amazon basins. Data from those samples are in agreement with those from the Central Amazon basin, except somewhat low gill-raker counts in specimens from the Madre de Dios drainage. *Satanoperca leucosticta* was described from the Essequibo River in Guyana. Kullander and Nijssen identified specimens from Suriname as *S. leucosticta*. *Satanoperca mapiritensis* is a widespread species in the Rio Orinoco basin. *Satanoperca pappaterra* is restricted to the Guaporé and Paraguay drainages. Additional undescribed species have been recognized, all within the Amazon basin. They are distinguished mainly by differences in colour pattern.

All material of the *S. jurupari* group available from the Orinoco and Negro basins and from Guyana and Suriname, including *S. mapiritensis* and *S. leucosticta*, is characterized by a pattern of small or large white spots on the sides of the head and commonly also on the snout. These white spots are persistent in preservative. Such white spots are absent in all material of the *S. jurupari* group from the southern and western part of the Amazon basin and the Paraguay-Paraná basin. In this material there may be iridescent spots present on the head in living or fresh specimens, but these spots do not persist in specimens preserved in formalin. *Satanoperca pappaterra* has neither white nor iridescent spots on the sides of the head.

The material of *Satanoperca* from French Guiana and adjacent state of Amapá clearly falls in the *S. jurupari* group of species, but a part of the material presents character states that are unique or rare within the genus, indicative of a separate species. What is problematic is that whereas the French Guiana specimens can be diagnosed by characters in combination, and are distinct from central Amazonian *S. jurupari*, they share no single fixed unique character state, i.e., no obvious autapomorphy, when compared with specimens from the geographically close Rio Amapá, which are morphologically intermediate.

Most species of *Satanoperca* have a long and deep snout and short postorbital head, giving them a characteristic appearance. In specimens from the Oyapock, Approuague, Comté, Kourou, Iracoubo, and Sinnamary, the snout appears proportionally longer than in other *Satanoperca*. The morphometric principal component analysis shows variation on the second component to be dominated by snout length and interorbital width (Tab. X, Fig. 5). The third component is dominated by caudal peduncle length. Caudal peduncle length and interorbital width mainly separate Central Amazonian from Amapá and French Guiana samples (Fig. 7). Snout length is variable but the visual estimate is supported by the biplot comparison (Fig. 8). Approuague and Oyapock specimens can be separated from the remaining geographical samples but the allocation of the Amapá samples remains contentious and the allocation of specimens from Comté, Kourou, Iracoubo, Sinnamary, and Kaw is ambiguous to some extent.

Consequently, whereas there is a clear structure in the ordering of the morphometric information, the PCA separating the extreme long-snouted specimens from the rest does not by itself provide obvious breaks. Interorbital width and snout length are decisive that the Approuague and Oyapock samples represent a species different from *S. jurupari*. Amapá specimens, on the other hand, are either too small for a decision or clearly group with *S. jurupari*. Comté and Kaw specimens appear to fall within the Amapá morphology (Figs 5-6).

The French Guiana samples tend to have lower meristics than *S. jurupari* and Amapá specimens. In specimens from French Guiana the modal dorsal-fin count of XV.9 is low and very unusual within the genus, in which XV.10 or XVI.9 is prevalent (Tab. VII). In French Guiana specimens with 10 soft rays, the last ray is unbranched, whereas it is usually branched in other species with XV.10. The modal E1 scale count is 26 among French Guiana specimens (Tab. IV). This number is somewhat frequent in Amapá samples, but extremely rare in other areas of distribution of the *S. jurupari* group in which 27 is prevalent. The number of gill-rakers externally on the first ceratobranchial (Tab. IX) is lower in French Guiana specimens (12-14) than in all other species of *Satanoperca* (usually 15-17) except the Madre de Dios sample of *S. jurupari* reported by Kullander (1986). It is also significantly lower in French Guiana than in Amapá specimens (15-17). The pectoral-fin count (Tab. VIII) averages low in French Guiana specimens (13), but the modal number is the same as in other samples of the *S. jurupari* group (14). The number of scale rows on the cheek (Tab. V) tends to be lower in French Guiana and Amapá samples (4-5) than in the Central Amazon (5-8, modally 6). All *S. jurupari* group species have the anal fin count III.7 with nearly no variation in soft ray numbers, so also the Amapá, French Guiana, and Central Amazonian materials.

Preserved specimens from French Guiana and Amapá invariably lack distinct white spots on the side of the head although at least in Amapá specimens slightly lighter areas can be discerned at the centre of some scales on the cheek and adjacent opercle. No differences were found in colour pattern between French Guiana, Amapá and Central Amazonian samples, although specimens from French Guiana tend to have less of dark spots in unpaired fins. Photographs of living specimens from French Guiana and Amapá (Keith *et al.* 2000; Stawikowski and Werner, 2004: 410; Aguirre *et al.*, 2011: 183) show specimens either with or without silvery spots on the sides of the head. Aquarium literature emphasizes the red lower lip in specimens from French Guiana and adjacent Amapá (Weidner, 2000; Stawikowski and Werner, 2004; Aguirre *et al.*, 2011) and this remains a potential colour synapomorphy, but the photo of a living aquarium specimen of *Satanoperca* imported from Manaus also shows red lower lip (Weidner, 2000: 225, Fig. 5).

Specimens from the Oyapock and Approuague rivers present character states that are undoubtedly autapomorphic within the genus and recovered from several samples representing different river systems. They include low meristics (low values for ceratobranchial gill rakers, soft dorsal fin rays, E1 scales) and proportions (long snout). Adjacent populations to the east include specimens representing plesiomorphic conditions, but it is uncertain what other autapomorphic condition those samples may possess. Specimens from other rivers in French Guiana generally have the low meristics of the Oyapock form. The sample from the Rio Amapá shares autapomorphic meristic conditions with French Guiana samples at low frequency. Specimens from the Rio Amapá and French Guiana are on the whole distinct from Central Amazonian *S. jurupari*, a species, however, for which no autapomorphic character states are known.

The specimens from the Uaçá and the Macari rivers group with the Central Amazonian *S. jurupari* in morphometrics and meristics, and are consequently referred to that species. The sample from the Juminán area consists mainly of small specimens, but with E1 scales 27 and D. XV.10, so they are also referred to *S. jurupari*. Remaining specimens from the state of Amapá are chiefly from the Cachoeira Grande in the Rio Amapá, and are intermediate between samples from French Guiana and *S. jurupari*. Specimens from Kaw are relatively deep-bodied and short-snouted and one of them has a very wide gill blade. The apparent mosaic of some meristics and the variation in snout length needs explanation, but based on available data only hypotheses can be formulated, and tested with larger series of well preserved specimens and genetic information. (1) Intermediate-looking specimens from coastal Amapá/French Guiana are hybrids between *S. rhynchitis* and *S. jurupari*. (2) Specimens from the Rio Amapá represent a distinct species for which I have missed some diagnostic character. (3) There is clinal variation from the Amazon up along the coast of the state of Amapá into French Guiana. (4) *S. rhynchitis* represents a rheophilic phenotype of a more widespread species in French Guiana and Amapá. None of these hypotheses can be satisfactorily tested with the material now available. The preferred current hypothesis about the data is that it signals a long-snouted endemic species with low meristics in French Guiana, compromised by coastal area hybridization with *S. jurupari*.

Hybridization and introgression are relatively little studied in South American fishes, although those phenomena are well documented from fishes in the northern hemisphere (e.g., Gante *et al.,* 2004; Freyhof *et al*., 2005). Menezes and Weitzman (1990) discussed the possible hybrid origin of the South American characid fish *Mimagoniates rheocharis* Menezes & Weitzman from *M. inequalis* (Eigenmann) and *M. microlepis* (Steindachner). They concluded that the presence of autapomorphies in *M. rheocharis* would speak against hybrid origin, but speculated nevertheless that these autapomorphies might have arisen after the hybridization-induced speciation event. Kullander *et al*. (2010) presented two specimens of *Crenicichla* that represent mixed morphological characters, and mitochondrial DNA from one of the putative parent species. Among fishes, hybrid individuals of first generations are probably naturally rare and easily recognized in groups of species exhibiting distinct morphological characteristics and colour patterns. Introgression from several generations past and hybrids between very similar species may both be more common especially in areas of secondary contact, and may be difficult to detect, passing for intraspecific variation. At least introgression evident in transfer of the mitochondrial genome seems to have occurred in the Amazonian genus *Symphysodon* (Ready *et al*., 2006), and several papers have reported hybrids or introgression in *Cichla*, although this includes both misidentifications and hybridization in transplanted stock in reservoirs (discussion in Kullander and Ferreira, 2006: 392; Oliveira *et al*., 2006; Willis *et al*., 2010; Macrander, 2010). Under the proposed scenario of a recent expansion from the Amazon into the Guianas, the variation in French Guiana and Amapá *Satanoperca* may fit a model of introgression resulting in mixed character states in some populations. There is, however, no evidence for hybridization of introgression within *Satanoperca*, in Amapá or elsewhere. Nevertheless, given that hybridization/introgression is documented, and probably underestimated, even fundamental to evolution (Dowling and Secor, 1997) and a likely component in range extension (Lewontin and Birch, 1966), and potentially contributing to “fuzziness” (Agapow *et al*., 2004: 172) affecting the species characterization, the requirement for samples to present fixed autapomorphic character states to be recognized as species may need to be relaxed (cf. Wiens and Serviedo, 2000). An alternative to introgression as source of fuzzy species borders would be clinal variation, a phenomenon indistinguishable from hybrid zones (Endler, 1977), but also a hypothesis which remains untestable at this time.

Since the Oyapock is rich in rapids the shape features may be explained as a specialization to life in fast-running water. There are collections of both *S. leucosticta* and *S. jurupari* from rapids elsewhere, and as these species do not show associated ecophenotypic variability, the shape features of *S. rhynchitis* are not recognized here as merely ecophenotypic variation.

Puyo’s (1949) description of *S. jurupari* from French Guiana is supplemented by a drawing of the head suggesting a relatively deep body, and short snout. The colour description mentions blue and yellow spots on the cheeks. Puyo apparently had only three specimens, 100-250 mm long from Saut Cafésoca (lower Oyapock, little downstream of Saut Grande Roche near St. Georges). The dorsal-fin count is given as XV.11. Specimens were obviously not preserved (Kullander and Nijssen, 1989: 172; Puyo, 1949: 7). The description deviates considerably from observations of *S. rhynchitis*, especially in the large size and the dorsal-fin count.

Gosse's (1976) comparative statistical analysis of *S. jurupari* agrees with the data presented here, showing significant differences between Amazonian *S. jurupari* and Oyapock material in meristics, and some body proportions.

French Guiana has species endemic to the Atlantic drainages of the Guianas, viz. *Cichla ocellaris* Schneider, *Crenicichla albopunctata* Pellegrin, *C. multispinosa* Pellegrin, *Geophagus harreri* Gosse, *Guianacara owroewefi* Kullander & Nijssen, *Geophagus surinamensis* (Bloch), *Krobia itanyi* (Puyo), *Nannacara anomala* Regan, and *N. aureocephalus* Allgayer. *Cichlasoma bimaculatum* (Linnaeus) extends into the lower Orinoco drainage, and *Cleithracara maronii* (Steindachner) has been recorded from the island of Trinidad. Two taxa represent species groups which have not yet been revised, namely *Crenicichla johanna* Heckel and *Aequidens tetramerus* (Heckel) which are reported from all over the Amazon basin as well as the Orinoco basin and the Guianas. In French Guiana, *C. johanna* is restricted to the Oyapock and Approuague drainages (Keith *et al.*, 2000; Le Bail *et al.*, 2012) indicating that it may actually be an unrecognized endemic taxon. The species identified as *Crenicichla saxatilis* (Linnaeus) from French Guiana (Ploeg, 1986) will need additional analysis. Five species are endemic to the Oyapock or Oyapock + Approuague, viz. *Geophagus camopiensis* Pellegrin, *Crenicichla ternetzi* Norman, *Guianacara geayi* (Pellegrin), *Krobia* sp., and *Retroculus septentrionalis* Gosse, with the caveat that a specimen probably representing *R. septentrionalis* has been collected in the Rio Araguari in the state of Amapá (pers. obs.). Originally known only from the Oyapock and Approuague, *Apistogramma gossei* Kullander has recently been reported from the Comté and Kourou (Le Bail *et al.*, 2012).

There is a definitive fauna shift between the Guianas and the Amazon basin marked by the Oyapock River, which is the most eastern river with the genus *Guianacara* Kullander & Nijssen, and with the several species endemic to the Oyapock or Oyapock+Approuague. Amazonian species have been reported from the lower Oyapock drainage in the Juminán swamps, some of them also recorded from the swampy areas around Kaw or even up to Iracoubo (Le Bail *et al.,* 2012): *Acaronia nassa* (Heckel), *Astronotus ocellatus* (Agassiz), *Chaetobranchopsis orbicularis* (Steindachner), *Chaetobranchus flavescens* (Heckel) *Cichla monoculus* Agassiz, *Cichlasoma amazonarum* Kullander, *Heros efasciatus* (Heckel), *Hypselecara temporalis* (Günther), *Laetacara* cf. *curviceps* (Ahl), *Mesonauta* cf. *guyanae* Schindler, and *Pterophyllum scalare* (Lichtenstein). *Heros efasciatus* was also known from around Kourou, as a probable result of an aquarium release (Keith *et al.*, 2000; P. Planquette, pers. comm.), and now colonised westward up to Iracoubo Yiyi marsh (Le Bail *et al.*, 2012). These 11 marginal taxa are numerically on a magnitude similar to the 18 species not occurring immediately east of the Oyapock. A widespread group of species like *Satanoperca jurupari* would be expected to occur along with the marginal taxa, whereas none of the endemic species would be expected to occur in the state of Amapá other than in right bank Oyapock tributaries.

Jégu and Keith (1999) documented a faunal limit in the lower Oyapock among otherwise Amazonian serrasalmid fishes, and discussed possible explanations, which are also valid for the cichlid taxa. They note that the Holocene deposits making up the coast of Amapá resemble the Amazonian várzea floodlands, thus extending the Amazonian biotopes in a wide coastal band in Amapá, whereas the marshy coastline of French Guiana west from the Oyapock is saline and dominated by alkaline water and mangrove, quite unlike the conditions in Amapá and the Guianas. They concluded that the Amazonian fishes extending to the lower Oyapock or waters immediately east of the lower Oyapock, occasionally to Kaw, most likely represent a progression of the Amazonian fauna with the formation of the Amapá marshlands. They did not comment on the Oyapock as an eastern limit of the Guianan fauna, however.

The distribution of *Satanoperca* in Amapá may conform to this pattern, with the added complication that a similar species is present in the Oyapock, and perhaps in the upper courses of Amapá rivers not yet sampled. This might provide a basis for hybridization, which is one possible explanation given above for the variation in morphology observed in some samples from coastal or Amapá localities.

Our understanding of the taxonomy and distribution of the Atlantic slope Guianan fish fauna is somewhat sketchy, although at least as far as cichlids are concerned species are as a rule endemic to Atlantic drainages and several genera are more or less endemic (*Cleithracara* Kullander & Nijssen, *Krobia* Kullander & Nijssen, *Guianacara, Nannacara* Regan). A species of *Guianacara* is also found in the upper Trombetas River (pers. obs.), and *G. dacrya* Arbour & López-Fernández occurs in both the Essequibo and Uraricoeira rivers (pers. obs.). A species of *Krobia* is also found in the Araguari River (pers. obs.), and another species is found in the upper Rio Xingu (Kullander, unpubl. data). *Nannacara* is a lowland genus with several species replacing each other along the coast from the southern bank of the mouth of the Amazon into the lower Orinoco, but with only patchy collecting records (pers. obs.). *Retroculus septentrionalis* is unlike other French Guiana cichlid endemics because it represents a genus with all the remaining species in southern tributaries of the Amazon basin (Kullander, 2003). Further collections in Brazilian areas adjacent to French Guiana may show more of expanded distributions or additional species in Amazonian or Amapá rivers.

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REFERENCES

AGAPOW P.M., BININDA-EMONDS O.R.P., CRANDALL K.A., GITTLEMAN J.L., MACE G.M., MARSHALL J.C. & PURVIS A., 2004. - The impact of species concept on biodiversity studies. *Quart. Rev. Biol.*, 79: 161-179.

AGUIRRE R., DE GASPERIS F., LONGY X., NANEIX F. & SÉVA A., 2011. - La Guyane française et ses cichlidés, 214 + 2 p. Fontourbière Saint Julia: Association France Cichlid.

CHIRICHIGNO N.F., 1963. - Estudio de la fauna ictiológica de los esteros y parte baja de los ríos del Departamento de Tumbes (Perú). *Serv. Pesq., Divulg. Cient.*, 22: 1-87.

DOWLING T.E. & SECOR C.L., 1997. - The role of hybridization in the evolutionary diversification of animals. *Ann. Rev. Ecol. Syst.*, 28: 593-619.

ENDLER J.A., 1977. - Geographic Variation, Speciation, and Clines. Monographs in Population Biology, 10: 246 p. Princeton, N.J.: Princeton Univ. Press.

FREYHOF J., LIECKFELDT D., PITRA C. & LUDWIG A., 2005. - Molecules and morphology: evidence for introgression of mitochondrial DNA in Dalmatian cyprinids. *Mol. Phyl. Evol.*, 37: 347-354.

GANTE H.F., COLLARES-PEREIRA M.J. & COELHO M.M., 2004. - Introgressive hybridisation between two Iberian *Chondrostoma* species (Teleostei, Cyprinidae) revisited: new evidence from morphology, mitochondrial DNA, allozymes and NOR-phenotypes. *Folia Zool.*, 53: 423-432.

GOSSE J.P., 1976. - Révision du genre *Geophagus*. *Mém., Acad. R. Sci. Outre-Mer, Cl. Sci. Nat. Méd., N.S.*, 19(3): 1-172.

GÜNTHER A., 1862. - Catalogue of the Fishes in the British Museum. Volume fourth. 534 p. London: Trustees [of the British Museum].

HUMPHRIES J.M., BOOKSTEIN F.L., CHERNOFF B., SMITH G.R., ELDER R.L. & POSS S.G., 1981. - Multivariate discrimination by shape in relation to size. *Syst. Zool.*, 30: 291-308.

JÉGU M. & KEITH P., 1999. - Le bas Oyapock limite septentrionale ou simple étape dans la progression de la faune des poissons d'Amazonie occidentale. *C. R. Acad. Sci., Paris, Sci. Vie*, 322: 1133-1143.

KEITH P., LE BAIL P.Y. & PLANQUETTE P., 2000. - Atlas des Poissons d'eau douce de Guyane. Tome 2, fascicule I: Batrachoidiformes, Mugiliformes, Beloniformes, Cyprinodontiformes, Synbranchiformes, Perciformes, Pleuronectiformes, Tetraodontiformes. 286 p. *Patrimoines Nat.*, 43(1). Paris: MNHN/SPN.

KULLANDER S.O., 1983. - A Revision of the South American Cichlid Genus *Cichlasoma*. 296 p. Stockholm: Swedish Museum of Natural History.

KULLANDER S.O., 1986. - Cichlid Fishes of the Amazon River Drainage of Peru. 431 p. Stockholm: Swedish Museum of Natural History.

KULLANDER S.O., 1998. - A phylogeny and classification of the South American Cichlidae (Teleostei: Perciformes). *In*: Phylogeny and Classification of Neotropical Fishes (Malabarba L.R., Reis R.E., Vari R.P., Lucena Z.M. & Lucena C.A.S., eds), pp. 461-498. Porto Alegre: Edipucrs.

KULLANDER S.O., 2003. - Family Cichlidae (Cichlids). *In*: Check List of the Freshwater Fishes of South and Central America (Reis R.E., Kullander S.O. & Ferraris C.J. Jr., eds), pp. 605-654. Porto Alegre: Edipucrs.

KULLANDER S.O. & FERREIRA E.J.G., 1988. - A new *Satanoperca* species from the Amazon River basin in Brazil. *Cybium*, 12: 343-355.

KULLANDER S.O. & FERREIRA E.J.G., 2006. - A review of the South American cichlid genus *Cichla*, with descriptions of nine new species (Teleostei: Cichlidae). *Ichthyol. Explor. Freshw.*, 17: 289-398.

KULLANDER S.O. & NIJSSEN H., 1989. - The Cichlids of Surinam. XXXIII + 256 p. Leiden and other cities: E.J. Brill.

KULLANDER S.O., NORÉN M., FRIÐRIKSSON G.B. & DE LUCENA C.A.S., 2010. - Phylogenetic relationships of species of *Crenicichla* (Teleostei: Cichlidae) from southern South America based on the mitochondrial cytochrome *b* gene. *J. Zool. Syst. Evol. Res.*, 48: 248-258.

LE BAIL P.Y., COVAIN R., JÉGU M., FISCH-MULLER S., VIGOUROUX R. & KEITH P., 2012. - Updated checklist of the freshwater and estuarine fishes of French Guiana. *Cybium*, 36(1): 293-319.

LEWONTIN R.C. & BIRCH L.C., 1966. - Hybridization as a source of variation for adaptation to new environments. *Evolution,* 20: 315-336.

LÓPEZ-FERNÁNDEZ H., WINEMILLER K.O. & HONEYCUTT R.L., 2010. - Multilocus phylogeny and rapid radiations in Neotropical cichlid fishes (Perciformes: Cichlidae: Cichlinae). *Mol. Phyl. Evol.*, 55: 1070-1086.

MACRANDER J.C., 2010. - Microsatellite development, population structure and demographic histories for two species of Amazonian Peacock Bass *Cichla temensis* and *Cichla monoculus* (Perciformes: Cichlidae). 80 p. Dissertations and Theses in Biological Sciences, School of Biological Sciences. Lincoln: Univ. of Nebraska.

MENEZES N.A. & WEITZMAN S.H., 1990. - Two new species of *Mimagoniates,* their phylogeny and biogeography and a key to the glandulocaudin fishes of Brazil and Paraguay. *Proc. Biol. Soc. Wash.*, 103: 380-426.

MOL J.H., VARI R.P., COVAIN R., WILLINK P.W. & FISCH-MULLER S., 2012. - Annotated checklist if the freshwater fishes of Suriname. *Cybium*, 36(1): 263-292.

OLIVEIRA A.V., PRIOLI A.J., PRIOLI S.M.A.P., BIGNOTTO T.S., JÚLIO JR. H.F., CARRER H., AGOSTINHO C.S. & PRIOLI L.M., 2006. - Genetic diversity of invasive and native *Cichla* (Pisces: Perciformes) populations in Brazil with evidence of interspecific hybridization. *J. Fish Biol.,* 69(Suppl. B): 260-277.

PLOEG A., 1986. - The fishes of the cichlid genus *Crenicichla* in French Guiana. *Bijdr. Dierk.*, 56: 221-231.

PUYO J., 1949. - Poissons de la Guyane française. Faune de l'Empire français. XII. 280 p. Paris: Office de la recherche scientifique d'outre-mer.

READY J.S., FERREIRA E.J.G. & KULLANDER S.O., 2006. - Discus fishes: mitochondrial DNA evidence for a phylogeographic barrier in the Amazonian genus *Symphysodon* (Teleostei: Cichlidae). *J. Fish Biol.*, 69(Suppl. B): 200-211.

REGAN C.T., 1906. - A revision of the South-American cichlid genera *Retroculus*, *Geophagus*, *Heterogramma*, and *Biotoecus*. *Ann. Mag. Nat. Hist.*, 17(7): 49-66.

SPSS, 2009. - PASW Statistics 18. Chicago, Illinois.

STAWIKOWSKI R. & WERNER U., 2004. - Die Buntbarsche Amerikas. Band 3: Erdfresser, Hecht- und Kammbuntbarsche. 478 p. Stuttgart: Verlag Eugen Ulmer.

WEIDNER T., 2000. - South American Eartheaters. 335 p. El Paso, Texas: Cichlid Press.

WIENS J.J. & SERVIEDO M.R., 2000. - Species delimitation in systematics: inferring diagnostic differences between species. *Proc. R. Soc. Lond. B*, 267: 631-636.

WILLIS S.C., NUNEZ M., MONTANA C.G., FARIAS I.P., ORTÍ G. & LOVEJOY N.R., 2010. - The Casiquiare river acts as a corridor between the Amazonas and Orinoco river basins: biogeographic analysis of the genus *Cichla*. *Mol. Ecol.,* 19: 1014-1030.